Bird assemblage changes along a savanna-rainforest gradient in north-eastern Australia

A.S. Kutt[1,2*] and E.P. Vanderduys[3]

[1.] School of BioSciences, University of Melbourne, Parkville, Victoria 3010, AUSTRALIA.

[2.] Bush Heritage Australia, Level 1, 395 Collins St, Melbourne, Victoria 3000, AUSTRALIA

[3.] CSIRO Land and Water Flagship, ATSIP PMB PO, Aitkenvale 4814, Queensland, AUSTRALIA.

[*]Author for correspondence: alex.kutt@bushheritage.org.au

ABSTRACT

Habitat and landscape gradients can provide insight on how vegetation pattern influence the composition and species turnover in birds. Gradients on mountainsides are particularly suitable as the vegetation can be distinctly stratified. On the western fall of the Australian wet tropics, the vegetation traverses through tropical savanna into tropical rainforest over a relatively short distance. We investigated bird richness and abundance in this transition. Seventeen sites were sampled from lowland (350 m) to upland (1000 m) locations, comprising six zones. Birds were sampled four times between 2006-2007. 125 species of birds representing 38 families were recorded. The pattern of abundance and richness along this gradient was characterised by second-order polynomial relationships. The nadir was where change in vegetation was most rapid; low open woodlands to dry open forest, between 500 and 800 m. We conclude that the avifauna assemblage we recorded along the gradient represents predominantly a woodland bird community that drifts upslope, an upland rainforest community that extends into adjacent tall forests, and an intermediate zone comprising a subset of the two communities. Very few species were ubiquitous. We conclude these intermediate zones may be important linking areas and habitat as climate change continues.

Introduction

Habitat patches and landscape gradients are two models used to conceptualise how species occupy landscapes and access the available resources (Fischer and Lindenmayer 2006). For highly mobile species, such as birds, both factors are influential (Price *et al.* 2009) and the relative effect of each will depend on local vegetation and landscape context (Cunningham *et al.* 2014). Mountains, and the changes in vegetation types with altitude and climate in these landscape features, provide natural systems for examining the determinants of species assemblage and the relative effect of discrete vegetation patches and gradients on vertebrate fauna (Bateman *et al.* 2010). There is generally a strong correlative relationship between elevation, climate and vegetation (Körner 2007) and zones of rapid transition in these factors can result in areas of increased or rapidly changing vegetation types and species (Heaney 2001).

Many studies of different biotic assemblages along vegetation gradients (often on mountains) have identified locations where there are spikes in species richness (e.g. McCain 2009). These peaks can occur at either points of optimal environmental conditions or at locations where contrasting vegetation communities occur in close proximity (i.e. ecotones) and many species' distributions overlap (Currie and Kerr 2008). In a global analysis of bird diversity patterns on mountains, temperature and water availability were strong determinants of the patterns recorded (McCain 2009). There are limited examples in Australia that use mountains to examine the turnover in bird communities with rapidly changing environmental conditions and vegetation, mostly due to the lack of locations with long elevation gradients. One example, in the snowline of the Australian alps, identified that changes in bird abundance and composition were mainly a function of the presence and disappearance of snow, rather than the contrasting vegetation structure (Osborne and Green 1992). More recently, a study in north-eastern Australia of birds in rainforests of increasing elevation, found species richness and abundance peaking in the locations of highest primary productivity, as measured by temperature and rainfall (Williams *et al.* 2010).

On the western fall of the Australian wet tropics, there is a gradient of vegetation that traverses through lowland tropical savanna into upland tropical rainforest over a very short distance. Here the change in vegetation types is rapid, in contrast to the areas of more continuous rainforests from sea level to the mountain tops on the eastern side. Studies on the dynamics of this western savanna-rainforest interface have previously focussed on vegetation at the rainforest-tall forest ecotone (Harrington and Sanderson 1994), small mammals (Bateman *et al.* 2010), and reptiles (Kutt *et al.* 2011). In this study we

examined the patterns of bird assemblage along a gradient from open savanna woodlands (~350 m) to upland rainforest (~1000 m). We investigated three questions with respect to bird distribution along this gradient: (1) does bird species richness and abundance change along the gradient of vegetation change?; (2) which bird species and families are strongly associated with particular vegetation types along the gradient?; and (3) are any observed changes in bird assemblage rapid (i.e. associated with habitat and vegetation patches) or gradual? This information may provide some insight into how predicted climate change might disrupt species distributions in different habitats (Braunisch et al. 2014).

Methods

Study area

The study sites were located on Mt Lewis (16°35'S, 145°16'E) in tropical north-eastern Queensland along an east-west altitudinal gradient (hereafter the gradient). The gradient extends from low rainfall (<600 mm y⁻¹) open savanna woodlands (300 m) in the west, to high rainfall (>3000 mm y⁻¹) upland (>1000 m) tropical rain forest to the east (Webb 1968) (Fig 1). The mountain peak experiences cooler temperatures (~19 °C mean annual temperature) and less precipitation seasonality (~80; coefficient of variation of mean monthly
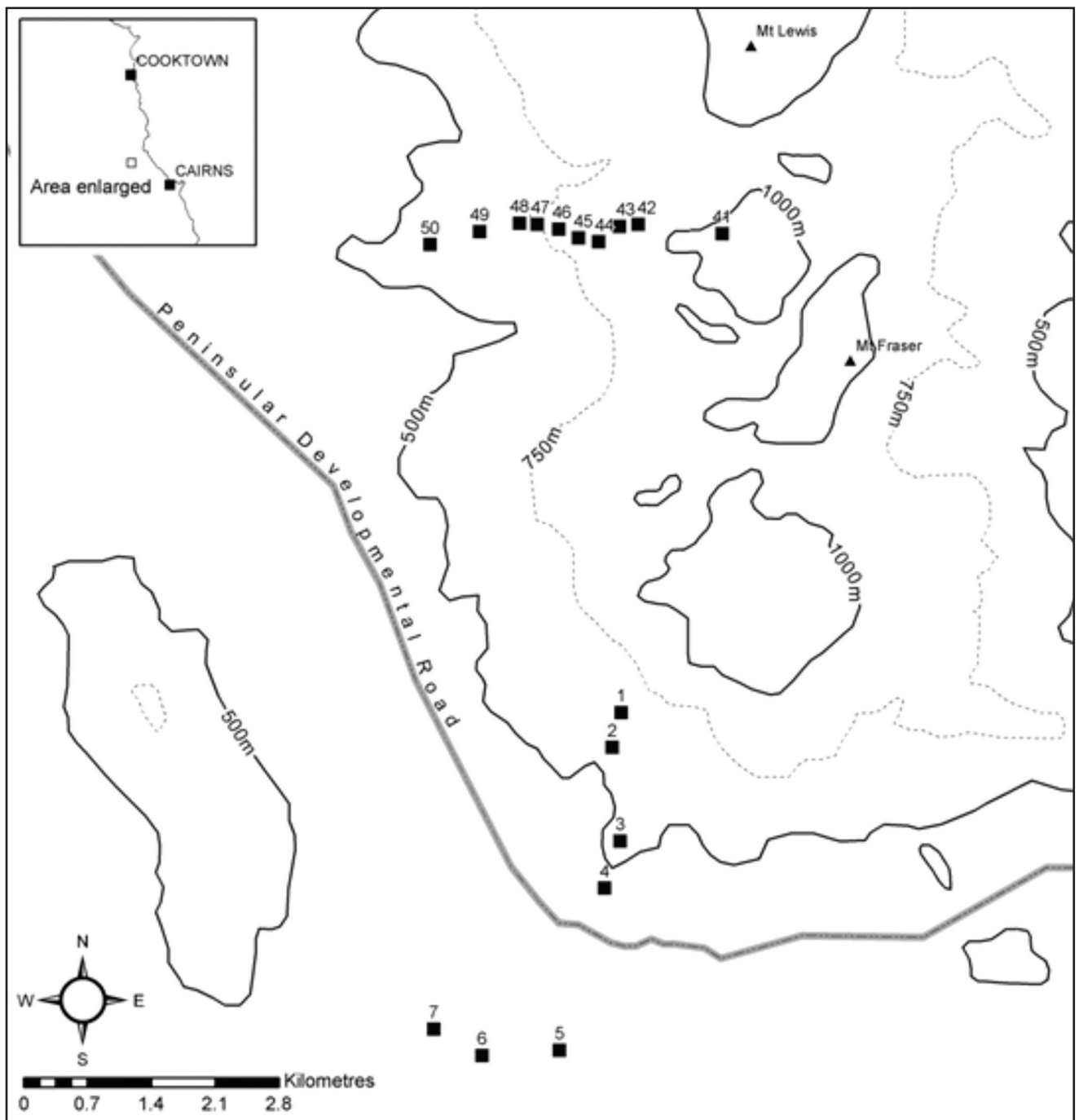

Figure 1. Location of sites and gradient sampled at Brooklyn Station in Queensland.

precipitation) than the base of the mountain (~22 °C, ~115) (climate data derived from ANUCLIM 5.1, McMahon *et al.* 1995). Since 2005, the study area has been managed by the Australian Wildlife Conservancy as a Nature Reserve, (Brooklyn Wildlife Sanctuary); previously it was operated as a pastoral lease for many years, with lowland habitats grazed by cattle.

Surveys

Seventeen sites were sampled on a gradient from lowland (350 m) to upland (1000 m) locations, and at each site we sampled the vegetation structure and habitat along a transect, and the bird community via area counts (Fig 1). Along the gradient there were six clear vegetation types changing with change in altitude. The vegetation types sampled were: complex notophyll vine forest and ecotone woodland of *Eucalyptus grandis* with understory rainforest elements (RFE, >900 m, two sites); *Eucalyptus resinifera, E. reducta, Corymbia intermedia, Syncarpia glomulifera, Allocasuarina torulosa* and *Banksia aquilonia* tall open forest (TOF, 800-900 m, four sites); *Eucalyptus reducta, E. portuensis, E. tereticornis, Corymbia intermedia, C. citriodora, C. stockeri* dry open forest (DOF, 700-800 m, three sites); *Eucalyptus portuensis, E. cullenii, Corymbia stockeri* open woodland (OW, 600-700 m, three sites; *Eucalyptus cullenii, E. granitica, E. leptophleba* low open woodland (LOW, 500-600 m , two sites); *Eucalyptus platyphylla* and *E. leptophleba* open alluvial woodland (OAW, 300-500 m, three sites). The capitalised structural code is referred to in the presentation of the results.

The vegetation and habitat variables were sampled at each site along the gradient following the methods outlined in Eyre *et al.* (2011) . At each site a 100 m transect was marked by two permanent steel fence posts at 0 and 100 m points running along the contour. For each stratum (canopy, sub-canopy and shrub) the crown cover was measured using a line intercept method; that is the length of the crown in each stratum along the 100 m transect is the estimate of percentage cover. The height of each strata was measured using a clinometer at the 0, 50 and 100 m points of the 100m tape and averaged. Five 1 m^2 quadrats along the 100 m transect were used to estimate percentage ground cover and rock cover.

The bird communities were surveyed in a 1-ha plot at each site along the gradient. To account for seasonal and inter-annual variation, surveys were conducted in both the late wet (April/May) and late dry (November) seasons, over four separate survey periods (May 2006, November 2006, April 2007 and November 2007). The survey method involves one experienced observer undertaking a five-minute count of all birds heard and seen within a 100 x 100 m plot, on eight separate occasions during each four-day survey period (Kutt *et al.* 2016; Perry *et al.* 2012). Consequently, there were a total of 32 bird counts for each site over the two years. Each of the eight counts were undertaken at different times of the day during a survey period;

two to three visits in the early morning (< 2 h after sunrise), two to three visits in the mid-morning (2 to 4 h after sunrise), and the remaining visits during less optimal times in the day (between 4 h after sunrise and 2 h before sunset). Birds detected outside of the plot were excluded, as were birds flying overhead, unless they were interacting with the habitat of the plot. We did not correct for detectability because the statistical biases introduced by those corrections are at least as large as not accounting for detectability (Mac Nally *et al.* 2014; Royle and Link 2006).

Statistical Analysis

Sample-based (observed) rarefaction curves were used to investigate the adequacy of our sampling effort. The number of observed species per vegetation type were plotted against the number of consecutive search days over the four survey periods (1-32 counts) in PRIMER 6 (Clarke and Gorley 2006). Sufficient sampling of sites was assumed to have been achieved if the curves approached the asymptote.

We examined the change in bird composition along the gradient via ordination. We constructed a Bray Curtis similarity matrix using fourth-root transformed abundance data in PRIMER (Clarke and Gorley 2006). We used non-metric multidimensional scaling to investigate the pattern in bird composition change in each vegetation types along the gradient.

The relationship between vegetation type / altitude and total bird species richness and abundance (pooled over all four sampling periods) was investigated by fitting the linear, non-linear and polynomial regression lines, and examining which had the best coefficient of determination or R-squared value.

The variation in mean site species richness and abundance, and individual species abundance (for those recorded in at least three surveys) in each of the six vegetation types along the gradient were examined using Kruskal-Wallis one-way analysis of variance. The variation in habitat structure across the vegetation types was also examined in this manner, and all analysis was undertaken using Statistica version 12 (StatSoft Inc. 2015).

Results

The species accumulation curves for all vegetation types approached the asymptote (not illustrated), indicating the sampling effort was adequate. The trajectory of change in bird composition as depicted by the ordination indicated a moderately clear turnover from the OAW to the RFE vegetation types (Fig. 2). The sites from 350-700 m form a loose cluster with some separation from the OAW, LOW and OW sites; then there is a change from the OW at 600-700 m through to the upland sites represented by forest (DOF-RFE) ecosystems (Fig. 2).
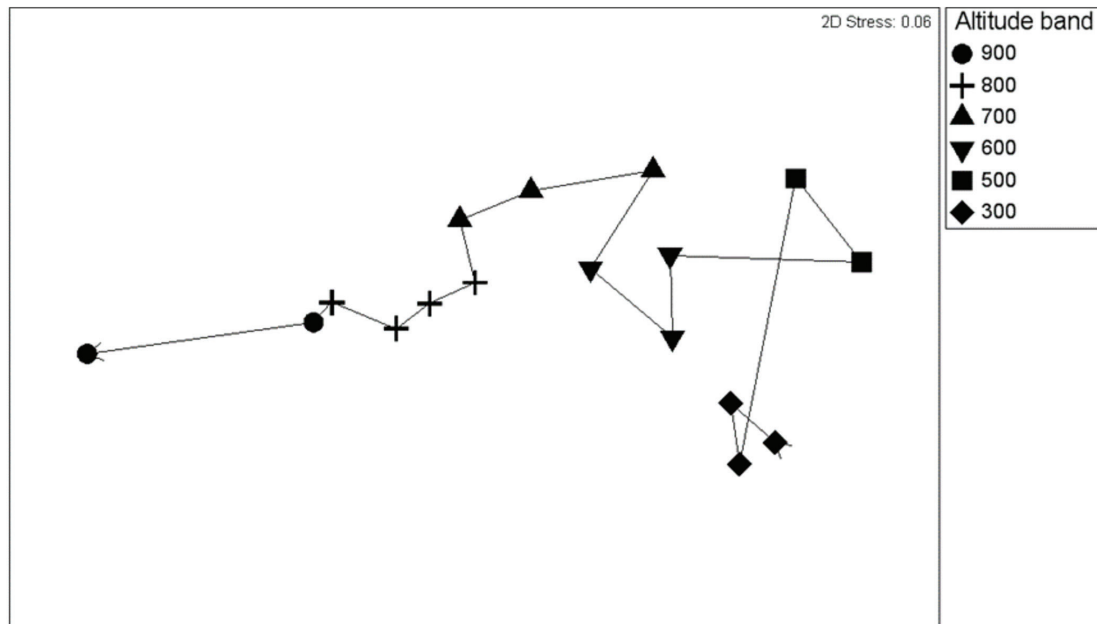
Figure 2. Two-dimensional ordination of survey sites using bird abundance data. Ordination used multi-dimensional scaling, root-transformed abundance data and Bray-Curtis similarity matrix. Ordination stress = 0.06. The trajectory line links the sites in order from the base to the top of the gradient. The relationship between altitude label and vegetation are as follows: 300 is 300-500 m, alluvial open woodland; 500 is 500-600 m, low open woodland; 600 is 600-700 m is open woodland; 700 is 700-800 m, dry open forest; 800 is 800-900 m, tall open forest; and 900 is >900 m rainforest / ecotone.

Vegetation structure varied significantly along the gradient, with reduced canopy and sub-canopy height at the lowest altitude AOW sites (16.3 m for canopy, 7.0 m for sub-canopy) in comparison to the high altitude TOF and RFE (28.5 m for canopy, 16.5 m for sub-canopy) (Table 1). Canopy and sub-canopy cover were highest within the upper altitude forest types (DOF, TOF; 68%-64.5% for canopy, 48.0%-54.5% for sub-canopy). Canopy cover declined in the open woodlands towards the lower section of the mountain gradient (23.5%-38.7%) as did the sub-canopy (9.3%-11.0%). Shrub cover was significantly higher in the DOF, TOF vegetation (12.5%-17.8%). The height and cover of the ground layer did not change significantly across vegetation types; however, rock cover was significantly higher in the transition from OW to DOF (18.0%-20.0%) (Table 1).

A total of 125 species of birds representing 38 families were recorded from bird surveys along the altitudinal gradient. The most abundant species were rainbow lorikeet *Trichoglossus haematodus*, spotted pardalote *Pardalotus punctatus*, mountain thornbill *Acanthiza katherina*, bridled honeyeater *Lichenostomus frenatus*, yellow-faced honeyeater *Lichenostomus chrysops*, scarlet honeyeater *Myzomela sanguinolenta*, white-throated honeyeater *Melithreptus albogularis*, white-naped honeyeater *Melithreptus lunatus* and mistletoebird *Dicaeum hirundinaceum*. The most ubiquitous across all sites were mistletoebird (n = 17 sites), rainbow lorikeet (n=16) and yellow-faced honeyeater, grey fantail *Rhipidura albiscapa*, cicadabird *Coracina tenuirostris*, (n=15 sites) bridled honeyeater, scarlet honeyeater, spotted pardalote, scaly-breasted lorikeet *Trichoglossus chlorolepidotus* and

Table 1. The variation in mean (and S.E.) site abundance and species richness, and habitat factors across the vegetation types using non-parametric analysis of variance. AOW = alluvial open woodland, LOW = low open woodland, OW = open woodland, DOF = dry open forest, TOF = tall open forest, RFE = rainforest / ecotone. * = P<0.05, ** = P<0.01, *** = P<0.001.

Variable	AOW (300-500m)	LOW (500-600m)	OW (600-700m)	DOF (700-800m)	TOF (800-900m)	RFE (>900m)	H	P
Number of sites	3	2	3	3	4	2		
Mean site abundance	196.7 (13.5)	60.5 (15.5)	110.0 (18.7)	188.3 (87.0)	296.3 (32.5)	399.0 (39.0)	11.6	*
Mean site species richness	41.7 (5.4)	24.0 (2.0)	29.0 (0.6)	25.3 (2.4)	39.0 (1.9)	44.0 (1.0)	13.3	*
Canopy height (m)	16.3 (0.7)	8.5 (0.5)	13.7 (2.4)	16.7 (0.3)	23.8 (3.5)	28.5 (6.5)	13.7	*
Sub-canopy height (m)	7.0 (1.0)	4.0 (1.0)	5.0 (0.6)	8.0 (0.1)	13.5 (3.7)	16.5 (1.5)	12.9	*
Shrub cover (%)	0	1.5 (0.5)	8.3 (3.3)	15.7 (2.2)	17.8 (6.6)	12.5 (2.5)	11.1	*
Rock cover (%)	0	4.0 (0.1)	18.0 (8.7)	20.0 (7.6)	9.3 (4.3)	2.0 (0.1)	11.3	*

white-bellied cuckoo-shrike *Coracina papuensis* (n=14). Honeyeaters (Meliphagidae) were the most abundant (1542 records) and species rich (n=16) family represented in the bird assemblage recorded during this study, followed by Psittacidae (382 records), Acanthizidae (235 records), Nectariniidae (153 records) and Petroicidae (145 records).

The relationship between species abundance and richness along the gradient was best characterised by second-order polynomial relationships (Fig. 3a-b). In each case the nadir was in the region where the vegetation types were narrow and shifted from LOW to OW and DOF. The mean site abundance was highest at the RFE (399.0 observations) and lowest in the LOW (60.5) (Table 2). The mean site species richness followed a similar pattern (44.0 in RFE, 24.5 at LOW), though species richness was also very high in the AOW (Table 2).

There was significant variation in species abundance along the gradient for many species, though the significance of this variation was generally very low (p<0.05-0.01, Table

2). As with the patterns of total bird abundance and species richness, many species were more abundant at the open woodlands at the bottom of the gradient (n=10) or at the top in the forests (n=14) (Table 2). Species that were more abundant in the open woodlands at the lower altitudes were common tropical savanna species such as peaceful dove *Geopelia striata* (mean = 14.0), noisy friarbird *Philemon corniculatus* (mean =24.0), and white-bellied cuckoo-shrike *Coracina papuensis* (mean =12.0); and species that were most abundant in the upper sites were tall and closed forest specialists such as the mountain thornbill *Acanthiza katherina* (mean = 38.5), bridled honeyeater (mean = 39.5), Lewin's honeyeater *Meliphaga lewinii* (mean = 25.0) (Table 2). There were very few species that peaked in abundance in the vegetation types in the intermediate zone where woodlands transitioned rapidly to forests, and some examples include the pied currawong *Strepera graculina* (LOW, 500-600 m), white-naped honeyeater (DOF, 700-800 m) and ecotonal / tall forest species such as the yellow-faced honeyeater and eastern yellow robin *Eopsaltria australis* (TOF, 800-900 m) (Table 2).
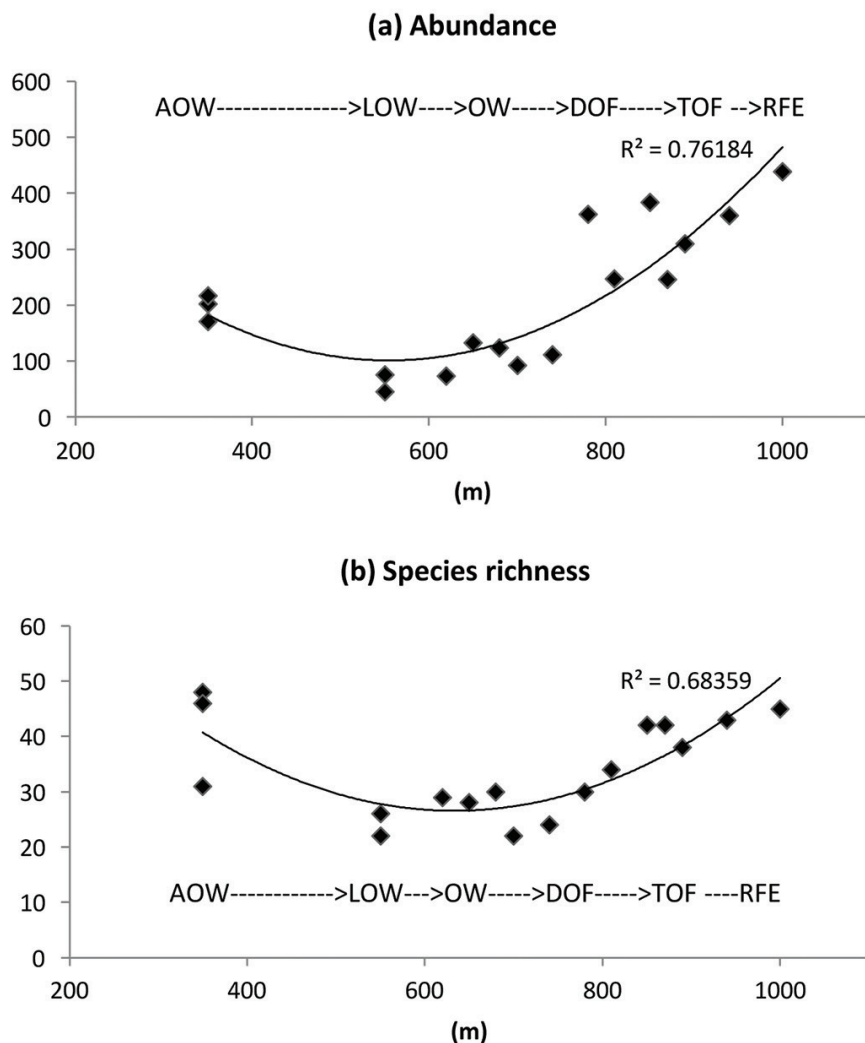
(a) Abundance

(b) Species richness

Figure 3. The relationship between bird abundance and species richness along the change in altitude / vegetation as identified by best fit trend lines: (a) Abundance, y = 693.9-2.12*x+0.0019*x2; and (b) Species richness, y = 97.53-0.22*x+0.0002*x2.

Table 2. The variation in mean (and S.E.) bird species abundance of bird species across the vegetation types. Significance tested by non-parametric analysis of variance, and only species and with significant variation are tabulated. n is the number of times recorded. * = P<0.05, ** = P<0.01, *** = P<0.001. AOW = alluvial open woodland, LOW = low open woodland, OW = open woodland, DOF = dry open forest, TOF = tall open forest, RFE = rainforest / ecotone.

Species	Common name	n	AOW (300-500m)	LOW (500-600m)	OW (600-700m)	DOF (700-800m)	TOF (800-900m)	RFE (>900m)	H	p
Geopelia striata	Peaceful Dove	3	14.0 (6.2)	0	0	0	0	0	15.8	**
Geopelia humeralis	Bar-shouldered Dove	3	1.0 (0.1)	0	0	0	0	0	16.0	**
Lopholaimus antarcticus	Topknot Pigeon	3	0	0	0	0	0.3 (0.3)	4.5 (0.5)	12.2	*
Cacatua galerita	Sulphur-crested Cockatoo	9	0	0	0.3 (0.3)	0.7 (0.3)	1.5 (0.5)	2.0 (1)	11.2	*
Scythrops novaehollandiae	Channel-Billed Cuckoo	3	0.3 (0.3)	1.0 (0.1)	0	0	0	0	11.7	*
Chalcites lucidus	Shining Bronze-cuckoo	4	0	0	0	0	0.5 (0.3)	2.0 (0.1)	12.0	*
Cacomantis variolosus	Brush Cuckoo	6	1.3 (0.3)	0	0	0	0.3 (0.3)	1.0 (0.1)	13.0	*
Dacelo leachii	Blue-Winged Kookaburra	3	2.0 (0.6)	0	0	0	0	0	15.8	**
Cormobates leucophaea	White-Throated Treecreeper	7	0	0	0	0.3 (0.3)	7.7 (2.6)	11.0 (3.0)	14.3	*
Sericornis magnirostra	Large-Billed Scrubwren	4	0	0	0	0	1.0 (0.6)	6.5 (4.5)	11.3	*
Gerygone mouki	Brown Gerygone	5	0	0	0	0	4.3 (1.5)	7.0 (0.1)	12.9	*
Acanthiza katherina	Mountain Thornbill	5	0	0	0	0	8.0 (2.9)	38.5 (9.5)	13.3	*
Acanthorhynchus tenuirostris	Eastern Spinebill	7	0	0	0	1.0 (1.0)	11.5 (2.6)	6.0 (5)	13.6	*
Meliphaga lewinii	Lewin's Honeyeater	12	0	0	1.0 (0.1)	2.3 (1.3)	7.3 (1.8)	25.0 (4)	15.2	**
Lichenostomus frenatus	Bridled Honeyeater	14	1.0 (1)	2.0 (2)	1.3 (0.3)	34.3 (30.8)	12.3 (2.1)	39.5 (5.5)	11.8	*
Lichenostomus chrysops	Yellow-faced Honeyeater	15	1.0 (0.6)	1.0 (0.1)	14.0 (6.7)	23.7 (9.4)	36.3 (1.9)	11.5 (11.5)	11.3	*
Lichmera indistincta	Brown Honeyeater	4	2.7 (2.2)	1.0 (0.1)	0	0	0	0	12.0	*
Melithreptus lunatus	White-naped Honeyeater	9	0	0	1.0 (1.0)	57.3 (35.3)	38.3 (21.5)	8.5 (8.5)	11.9	*
Entomyzon cyanotis	Blue-faced Honeyeater	3	2.0 (1.0)	0	0	0	0	0	15.9	**
Philemon corniculatus	Noisy Friarbird	11	24.0 (4.4)	2.0 (1)	5.3 (4.3)	1.0 (0.6)	0.3 (0.3)	0	12.4	*
Philemon citreogularis	Little Friarbird	7	5.7 (0.9)	1.5 (0.5)	1.7 (1.7)	0.3 (0.3)	0	0	11.5	*
Microeca flavigaster	Lemon-bellied Flycatcher	3	4.7 (0.7)	0	0	0	0	0	15.9	**
Eopsaltria australis	Eastern Yellow Robin	9	0	0	0.3 (0.3)	2.3 (0.7)	16.3 (2.1)	8.5 (8.5)	12.1	*
Psophodes olivaceus	Eastern Whipbird	5	0	0	0	0	0.8 (0.3)	8.0 (3)	13.4	*
Pachycephala pectoralis	Golden Whistler	5	0	0	0	0	8.0 (4.8)	9.5 (1.5)	12.4	*

Species	Common name	n	AOW (300-500m)	LOW (500-600m)	OW (600-700m)	DOF (700-800m)	TOF (800-900m)	RFE (>900m)	H	p
Pachycephala rufiventris	Rufous Whistler	4	1.0 (0.1)	0	0.7 (0.7)	0	0	0	11.2	*
Machaerirhynchus flaviventer	Yellow-breasted Boatbill	3	0	0	0	0	0.3 (0.3)	2.5 (1.5)	11.6	*
Rhipidura albiscapa	Grey Fantail	15	3.0 (2)	0	1.3 (0.3)	1.0 (0.1)	3.3 (0.3)	13.5 (7.5)	12.5	*
Coracina lineata	Barred Cuckoo-shrike	5	0	0	0	0	1.0 (0.4)	3.5 (2.5)	12.5	*
Coracina papuensis	White-bellied Cuckoo-shrike	14	12.0 (2.1)	2.5 (0.5)	7.3 (1.9)	1.0 (0.1)	1.3 (0.5)	0	14.1	*
Coracina tenuirostris	Cicadabird	15	1.0 (0.1)	0.5 (0.5)	2.3 (0.9)	3.0 (1)	4.3 (0.9)	0.5 (0.5)	11.2	*
Strepera graculina	Pied Currawong	13	0	5.0 (3)	1.0 (0.1)	1.7 (0.7)	1.3 (0.3)	0.5 (0.5)	12.3	*
Ptiloris victoriae	Victoria's Riflebird	4	0	0	0	0	0.5 (0.3)	4.5 (2.5)	11.9	*
Neochmia temporalis	Red-Browed Finch	6	0	0	0	0	8.8 (2.7)	6.5 (4.5)	15.2	**
Dicaeum hirundinaceum	Mistletoebird	17	2.7 (0.7)	3.0 (2.0)	10.3 (3.0)	13.3 (1.9)	15.5 (2.9)	3.0 (2.0)	12.3	*

Discussion

Our study demonstrated that for our gradient that traversed a range of broadly distinct tropical vegetation communities, and where there was a relatively rapid change from tropical savanna woodlands to structurally complex tall open and closed forests, species richness and abundance was generally lowest in this transition zone, and was highest at the two ends of the spectrum. We found that the zone of greatest vegetation heterogeneity (i.e. of most rapid change in vegetation types), was not the area of greatest species richness or abundance. There was a consistent change in beta diversity from one end of the altitude gradient to the other. As a general rule, avifaunal species richness increases with greater architectural complexity in vegetation in both dry (Kutt and Martin 2010), and wet forests (Hurlbert 2004), but in our study the peaks were at either end of the gradient, in the most complex and the least complex vegetation types. In contrast, gradients in continuous rainforests in north eastern Australia, total species richness and abundance peaks between 600 to 1000 m, the areas of highest measured productivity (Williams *et al.* 2010). For our savanna-rainforest gradient, the area of highest diversity is not the point of greatest environmental and vegetation heterogeneity unlike other studies (Currie and Kerr 2008; Hawkins *et al.* 2005), but instead the locations where the vegetation units occurs in large tracts (i.e. savannas, rainforest). The areas of rapid vegetation change on the mountain side seems to be unsuitable for a resident avifauna, perhaps due to resource constraints, reduced productivity and possibly fire history (Harrington and Sanderson 1994; Smith *et al.* 2014; Stanton *et al.* 2014).

There are a range of global patterns of montane bird diversity recorded (McCain 2009) and our data did not conform to any very clearly; however our gradient truncated at 1000 m and accurate assessment of a montane patterns require continuous gradients to higher altitudes (McCain 2005; Nogues-Bravo *et al.* 2008). Data collected in upland rainforest beyond the end of our survey gradient suggests that both abundance and species richness would have declined with increasing altitude, had we continued our survey further into the rainforest at upper altitudes (Williams *et al.* 2010). A comparison of our patterns with that of Williams *et al.* (2010), which sampled a rainforest-only gradient eastern side of the Mt Lewis, opposite to the location of our gradient, indicated contrasting patterns; that in rainforests on the eastern fall of this mountain the peak in bird diversity was in the mid-altitudes, whereas for a gradient that traverses woodland to rainforest, the peaks are with the most distinct vegetation types. In previous surveys along this savanna-rainforest gradient, Bateman *et al.* (2010) recorded a largely linear increase in small mammal richness and abundance from lowland to upland sites while lizard diversity peaked at low to mid altitudes, even though abundance of each species was low (Kutt *et al.* 2011). For mammals the authors concluded that the small mammal assemblage changed gradually through the habitat types without any clear pattern of disjunction, and the increasing diversity was associated with increasing habitat heterogeneity and rainfall (Bateman *et al.* 2010).

Our bird data suggest that the patterns we recorded were a function of resource security or consistency in the savannas and rainforests (e.g. seeds, fruits, diverse range of flowering species and regular water sources)

and the rapid transition in vegetation types and the associated habitat heterogeneity in the narrow band between the highest and lowest points, represent a reduction in available resources for certain functional groups such as granivores, insectivores and nectarivores (Kissling *et al.* 2008; Şekercioḡlu *et al.* 2002). There is possibly also a degree of resource inconsistency in these intermediate zones, for example periods of flowering or fruiting, which attract species that migrate locally, but do not remain sedentary at the site (Wolfe *et al.* 2014). In contrast, after extensive examination of multiple global patterns in montane diversity and richness, there is now a belief that many patterns in species richness and species turnover, are largely idiosyncratic and inconsistent (McCain and Beck 2016).

There is likely to be a link between the habitat structure at each site and the bird species or assemblage recorded in those sites. Vegetation structural diversity is a well-accepted coarse predictor of bird community richness and composition and one expects some increases in species richness with increasing structural complexity (Kutt and Martin 2010; Whelan 2001). In contrast there can be spatial and temporal variation due to changing local vegetation pattern (Price *et al.* 2009). In this study, the vegetation structural complexity did increase from the AOW sites to the RFE sites, and there was a clear turnover in the composition of the birds from the savanna to the rainforest. The shift in species included an increase in small bodied insectivorous species (e.g. *Sericornis, Acanthiza Gerygone*), that forage on the ground and in the shrub layer, and an increase in frugivorous species (e.g. Topknot Pigeon, Victoria's Riflebird) associated with an increase in rainforest plant species. In the more savanna sites, there were a greater number of species with foraging strategies better suited to open habitats, such as terrestrial granivores (e.g. pigeons) and perching and gleaning species (e.g. cuckoo-shrikes, whistlers, kookaburras). In our study, the patterns of bird abundance and species richness is a combination of the climate and altitudinal controls on vegetation pattern on the gradient, the changing structure of this vegetation and the evolution of xeric / savanna and mesic / rainforest adapted species within widespread Australian bird genera (Byrne *et al.* 2011).

Many species, predominantly nectarivores in the Meliphagidae family, seasonally migrate from upland rainforest to lowland rainforest, or tall wet forests and dry woodlands tracking resources (Anderson *et al.* 2013; Chapman and Harrington 1997). The high number of honeyeaters recorded, and local migration patterns, might also contribute to higher diversity at each end of the gradient and the lower intermediate altitude species richness and abundance; these low open woodlands and forests may serve more as transition zones between more

extensive and resource rich areas of habitat (McCain 2009; Shoo *et al.* 2006). The higher bird diversity at the rainforest-forest edge is also a function of two contrasting vegetation types and an edge effect where rainforest species partially utilise these adjacent sites (Lomolino 2001; Murcia 1995).

In conclusion, the avifauna assemblage we recorded along this savanna-rainforest gradient represents a largely woodland bird community that drifts upslope in distribution, an upland rainforest community that extends into adjacent tall forests, and an intermediate zone where there is a depauperate subset of species from the rainforest and savanna communities. However, we recognise that this study only sampled a single gradient on the western fall of the wet tropics, and the patterns may not be universal, especially where the other gradients might be more extensive, vegetation types are different, and the slope of the gradient may be more gradual. There are only a few ubiquitous species along the gradient (e.g. Mistletoebird) and migratory species from the upland and lowland sites (e.g. Bridled Honeyeater). What is noteworthy is the relative equality of bird species richness in the lowlands tropical savanna sites (less complex vegetation) and the rainforest-wet forest ecotones, suggesting these savannas are an important habitat for avifauna. There are two possible reasons why in this study, these contrasting vegetation types may have an equal pattern. Firstly, species richness is strongly correlated with climate (Boucher-Lalonde *et al.* 2014) and our multi-year seasonal sampling captured both the winter and summer avifauna of the savannas (Kutt *et al.* 2012), whereas the rainforest bird community was more stable. Secondly, as indicated previously, the diversification of many Australian birds, in response to shifting size of mesic and arid zones, has resulted in many genera and families having both savanna and closed forest species and specialists, rather than each having distinct endemic species (Byrne *et al.* 2011; Byrne *et al.* 2008).

From a conservation perspective, though these rapidly changing zones of dry open forests and woodlands are perhaps not significant habitat for the avifauna in their own right, the function they play in connecting two disparate but large areas of continuous habitat are probably significant (Lindenmayer *et al.* 2010). For example climate change induced changes in weather patterns may alter species distributions, resource availability and timing of local migrations; and linking zones will be important conduits and habitat in their own right (Sekercioglu *et al.* 2008). Fire management in these areas bridging fire prone and fire resistant vegetation is important, as shifts in regime can reduce or increase rainforest area, and therefore bird community assemblage (Chapman and Harrington 1997; Little *et al.* 2012).

Acknowledgments

References

Anderson, A.S., Storlie, C.J., Shoo, L.P., Pearson, R.G., and Williams, S.E. 2013. Current analogues of future climate indicate the likely response of a sensitive montane tropical avifauna to a warming world. *PLoS ONE* **8**: e69393.

Bateman, B.L., Kutt, A.S., Vanderduys, E.P., and Kemp, J.E. 2010. Small-mammal species richness and abundance along a tropical altitudinal gradient: an Australian example. *Journal of Tropical Ecology* **26**: 139-149.

Boucher-Lalonde, V., Kerr, J.T., and Currie, D.J. 2014. Does climate limit species richness by limiting individual species' ranges? *Proceedings of the Royal Society B: Biological Sciences* **281**.

Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Zellweger, F., and Bollmann, K. 2014. Temperate mountain forest biodiversity under climate change: compensating negative effects by increasing structural complexity. *PLoS ONE* **9**: e97718.

Byrne, M., Steane, D.A., Joseph, L., Yeates, D.K., Jordan, G.J., Crayn, D., Aplin, K., Cantrill, D.J., Cook, L.G., Crisp, M.D., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P., and Weston, P.H. 2011. Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography* **38**: 1635-1656.

Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., Cooper, S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N., and Wyrwoll, K.H. 2008. Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology* **17**: 4398-4417.

Chapman, A., and Harrington, G.N. 1997. Responses by birds to fire regime and vegetation at the wet sclerophyll/tropical rainforest boundary. *Pacific Conservation Biology* **3**: 213.

Clarke, K.R., and Gorley, R.N. 2006. *PRIMER v6 User Manual and Program.* (PRIMER-E Ltd: Plymouth UK)

Cunningham, R.B., Lindenmayer, D.B., Crane, M., Michael, D.R., Barton, P.S., Gibbons, P., Okada, S., Ikin, K., and Stein, J.A.R. 2014. The law of diminishing returns: woodland birds respond to native vegetation cover at multiple spatial scales and over time. *Diversity and Distributions* **20**: 59-71.

Currie, D.J., and Kerr, J.T. 2008. Tests of the mid-domain hypothesis: a review of the evidence. *Ecological Monographs* **78**: 3-18.

Eyre, T.J., Kelly, A.L., Neldner, V.J., Wilson, B.A., Ferguson, D.J., Laidlaw, M.J., and Franks, A.J. 2011. *BioCondition; A Condition Assessment Framework for Terrestrial Biodiversity in Queensland. Assessment Manual. Version 2.1.* (Department of Environment and Resource Management (DERM), Biodiversity and Ecosystem Sciences.: Brisbane)

Fischer, J., and Lindenmayer, D.B. 2006. Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos* **112**: 473-480.

Harrington, G.N., and Sanderson, K.D. 1994. Recent contraction of wet sclerophyll forest in the wet tropics of Queensland due to invasion by rainforest. *Pacific Conservation Biology* **1**: 319-327.

Hawkins, B.A., Diniz-Filho, J.A.F., and Weis, A.E. 2005. The mid-domain effect and diversity gradients: Is there anything to learn? *American Naturalist* **166**: 140-143.

Heaney, L.R. 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology & Biogeography* **10**: 15-39.

Hurlbert, A.H. 2004. Species–energy relationships and habitat complexity in bird communities. *Ecology Letters* **7**: 714-720.

Kissling, W.D., Field, R., and Böhning-Gaese, K. 2008. Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects? *Global Ecology and Biogeography* **17**: 327-339.

Körner, C. 2007. The use of 'altitude' in ecological research. *TRENDS in Ecology and Evolution* **22**: 569-574.

Kutt, A.S., Bateman, B.L., and Vanderduys, E.P. 2011. Lizard diversity on a rainforest–savanna altitude gradient in north-eastern Australia. *Australian Journal of Zoology* **59**: 86-94.

Kutt, A.S., and Martin, T.G. 2010. Bird foraging height predicts bird species response to woody vegetation change. *Biodiversity and Conservation* **19**: 2247-2262.

Kutt, A.S., Perkins, G.C., Colman, N., Vanderduys, E.P., and Perry, J.J. 2012. Temporal variation in a savanna bird

assemblage: what changes over 5 years? *Emu* **112**: 32-38.

Kutt, A.S., Vanderduys, E.P., Perry, J.J., Mathieson, M.T., and Eyre, T.J. 2016. Yellow-throated miners Manorina flavigula homogenize bird communities across intact and fragmented landscapes. *Austral Ecology* **41**: 316-327.

Lindenmayer, D.B., Steffen, W., Burbidge, A.A., Hughes, L., Kitching, R.L., Musgrave, W., Smith, M.S., and Werner, P.A. 2010. Conservation strategies in response to rapid climate change: Australia as a case study. *Biological Conservation* **143**: 1587-1593.

Little, J.K., Prior, L.D., Williamson, G.J., Williams, S.E., and Bowman, D.M.J.S. 2012. Fire weather risk differs across rain forest—savanna boundaries in the humid tropics of northeastern Australia. *Austral Ecology* **37**: 915-925.

Lomolino, M.V. 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* **10**: 3-13.

Mac Nally, R., Kutt, A.S., Eyre, T.J., Perry, J.J., Vanderduys, E.P., Mathieson, M., Ferguson, D.J., and Thomson, J.R. 2014. The hegemony of the 'despots': the control of avifaunas over vast continental areas. *Diversity and Distributions* **20**: 1071-1083.

McCain, C.M. 2005. Elevational gradients in diversity of small mammals. *Ecology* **86**: 366-372.

McCain, C.M. 2009. Global analysis of bird elevational diversity. *Global Ecology and Biogeography* **18**: 346-360.

McCain, C.M., and Beck, J. 2016. Species turnover in vertebrate communities along elevational gradients is idiosyncratic and unrelated to species richness. *Global Ecology and Biogeography* **25**: 299-310.

McMahon, J.P., Hutchinson, M.F., Nix, H.A., and Ord, K.D. 1995. *ANUCLIM User's Guide, Version 1.* (Australian National University: Canberra)

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution* **10**: 58-62.

Nogues-Bravo, D., Araujo, M.B., Romdal, T., and Rahbek, C. 2008. Scale effects and human impact on the elevational species richness gradients. *Nature* **453**: 216-219.

Osborne, W., and Green, K. 1992. Seasonal changes in composition, abundance and foraging behavior of birds in the snowy mountains. *Emu* **92**: 93-105.

Perry, J.J., Kutt, A.S., Perkins, G.C., Vanderduys, E.P., and

Colman, N.J. 2012. A bird survey method for Australian tropical savannas. *Emu* **112**: 261-266.

Price, B., McAlpine, C.A., Kutt, A.S., Phinn, S.R., Pullar, D.V., and Ludwig, J.A. 2009. Continuum or discrete patch landscape models for savanna birds? Towards a pluralistic approach. *Ecography* **32**: 745-756.

Royle, J.A., and Link, W.A. 2006. Generalized site occupancy models allowing for false positive and false negative errors. *Ecology* **87**: 835-841.

Şekercioğlu, Ç.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., and Sandí, R.F. 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences* **99**: 263-267.

Şekercioğlu, C.H., Schneider, S.H., Fay, J.P., and Loarie, S.R. 2008. Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* **22**: 140-150.

Shoo, L.P., Williams, S.E., and Hero, J.M. 2006. Detecting climate change induced range shifts: Where and how should we be looking? *Austral Ecology* **31**: 22-29.

Smith, G., Fensham, R., Ferguson, D., Hogan, L., and Mathieson, M. 2014. Fauna of the grassland-forest landscape mosaics of the Bunya Mountains, eastern Australia. *Australian Zoologist* **37**: 302-310.

Stanton, P., Stanton, D., Stott, M., and Parsons, M. 2014. Fire exclusion and the changing landscape of Queensland's Wet Tropics Bioregion 1. The extent and pattern of transition. *Australian Forestry* **77**: 51-57.

StatSoft Inc. 2015. *STATISTICA (data analysis software system), version 12. 1983-2015.* In '.' (www.statsoft.com: Tulsa, OK)

Webb, L.J. 1968. Environmental relationships of the structural types of Australian rainforest vegetation. *Ecology* **49**: 296-311.

Whelan, C.J. 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology* **82**: 219–231.

Williams, S.E., Shoo, L.P., Henriod, R., and Pearson, R.G. 2010. Elevational gradients in species abundance, assemblage structure and energy use of rainforest birds in the Australian Wet Tropics bioregion. *Austral Ecology* **35**: 650-664.

Wolfe, J.D., Johnson, M.D., and Ralph, C.J. 2014. Do birds select habitat or food resources? nearctic-neotropic migrants in northeastern Costa Rica. *PLOS ONE* **9**: e86221.